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The earliest fossil record of Panorpidae (Mecoptera) from the Middle Jurassic of China

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Abstract

The early history of Panorpidae (Mecoptera) is poorly known due to sparse fossil records. Up to date, only nine fossil species have been described, all from the Paleogene, except the Early Cretaceous *Solusipanorpa gibbidorsa* Lin, 1980. However, we suggest *S. gibbidorsa* is too incompletely preserved to permit even family classification. A new genus with two new species, *Jurassipanorpa impunctata* **gen. et sp. n.** and *Jurassipanorpa sticta* **sp. n.**, are described based on four well-preserved specimens from the late Middle Jurassic Jiulongshan Formation of Daohugou, Inner Mongolia, China. These two new species are the earliest fossil records of Panorpidae. The new genus is erected based on a combination of forewing characters: both R_1 and Rs_1 with two branches, 1A reaching posterior margin of wing distad of the forking of Rs from R_1, and no crossveins or only one crossvein between veins of 1A and 2A. In all four specimens, long and robust setae ranging from 0.09 to 0.38 mm in length and pointing anteriorly, are present on anal veins of forewings. The function of these setae is enigmatic.

Keywords

Jurassipanorpa, new genus, new species, Jiulongshan Formation, Daohugou

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Introduction

Mecoptera is a small order of insects, comprising about 600 extant species assigned to nine families (Cai et al. 2008, Krzemiński and Soszyńska-Maj 2012). The Panorpidae is the largest family in the order, with about 400 extant species in six genera: *Panorpa* Linnaeus, 1758, *Leptopanorpa* MacLachlan, 1875, *Neopanorpa* Weele, 1909, *Sinopanorpa* Cai, Huang & Hua, 2008, *Furcatopanorpa* Ma & Hua, 2011 and *Dicerapanorpa* Zhong & Hua, 2013 (Byers 1967, Cai et al. 2008, Cai and Hua 2009, Ma and Hua 2011, Zhong and Hua 2013).

Fossil records of the Panorpidae are fairly rare. Up to date, only three genera have been described in this family and two of them are fossil-only genera: *Solusipanorpa* Lin, 1980 with one species from the Early Cretaceous of China (Lin 1980); *Baltipanorpa* Krzemiński, 2012 with one species from the Eocene Baltic amber (Krzemiński and Soszyńska-Maj 2012); and *Panorpa* Linnaeus, 1758 with seven species from Baltic amber, Eocene of U.S.A. and Oligocene of Germany (Carpenter 1931, Statz 1936, Carpenter 1954). However, the holotype (and the only known specimen) of *Solusipanorpa gibbidorsa* is too incompletely preserved and cannot be attributed to any particular family. In addition, Archibald et al. (2013: fig. 23) reported several undescribed specimens of Panorpidae in the Early Eocene Okanagan Highlands, Canada and U.S.A. Therefore, with *Solusipanorpa gibbidorsa* ignored, the fossil records of Panorpidae are known so far since the Early Eocene.

Recently we collected four well-preserved fossils, which we attribute to Panorpidae, from the Jiulongshan Formation at Daohugou, Ningcheng County, Inner Mongolia, China. The Jiulongshan Formation is dated as the late Middle Jurassic, ca. 165 Ma (Ren et al. 1995, 2002, Shen et al. 2003, Chen et al. 2004, Liu et al. 2004, Ji et al. 2006, Gao and Ren 2006, Huang et al. 2006, Wang et al. 2013). Based on a combination of forewing characters: both R_1 and Rs_1 with two branches, 1A reaching posterior margin of wing distad of the forking of Rs from R_1, and no crossveins or only one crossvein between veins 1A and 2A, we erect a new genus *Jurassipanorpa* with two new species.

Materials and methods

This study is based on four fossil specimens collected from the late Middle Jurassic Jiulongshan Formation at Daohugou Village of Ningcheng County in Inner Mongolia, China. All type specimens are housed in the fossil insect collection of the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator).

The specimens were examined and photographed using a Leica MZ12.5 dissecting microscope with a Leica DFC 500 digital camera and illustrated with the aid of a drawing tube attachment. The line drawings were drawn by Adobe Photoshop CS5. We use the venational nomenclature of Willmann (1989).

Systematic Palaeontology

Order Mecoptera Packard, 1886
Family Panorpidae Latreille, 1805

Jurassipanorpa **Ding, Shih & Ren, gen. n.**
http://zoobank.org/5D919FDF-18E3-48D5-B723-2BDCE98B900B

Etymology. The generic name is a combination of Jurassic, highlighting the age of these fossil panorpids, and *Panorpa*, the type genus of Panorpidae. Gender feminine.

Type species. *Jurassipanorpa impunctata* Ding, Shih & Ren, sp. n.

Other included species. *Jurassipanorpa sticta* Ding, Shih & Ren sp. n.

Diagnosis. In forewing, Sc reaching the anterior margin near or beyond the middle of the wing; both R_1 and Rs_1 with two branches; 1A reaching posterior margin distad of the forking of Rs from R_1; 3 anal veins present; one crossvein between Cu_1 and Cu_2 and between 1A and 2A respectively.

Remarks. We assigned this genus to Panorpidae mainly based on the following characters: (1) head capsule with prolonged downward mouthparts; (2) slender wings and forewing slightly larger than hind wing with similar veins; (3) forewing Rs with five branches; (4) forewing M with four branches; (5) forewing Cu_1 not fused with M basally, one crossvein between M_4 and Cu_1; and (6) hind wing Rs with five and M with four branches as those of forewing.

Jurassipanorpa impunctata **Ding, Shih & Ren, sp. n.**
http://zoobank.org/021EE774-F1FC-4C91-A91F-7E39A5B82809
Figs 1, 2

Etymology. From the Latin *impunctata*, meaning no spots, referring to the fact that no spots and fasciae on all wings.

Holotype. CNU-MEC-NN-2013006, a well-preserved female specimen with body and wings, but legs poorly preserved.

Paratype. CNU-MEC-NN-2013012 P/C, sex unknown, with well-preserved legs, but four wings overlapping almost entirely and abdomen partially preserved.

Locality and horizon. Jiulongshan Formation, late Middle Jurassic; Daohugou Village, Ningcheng County, Inner Mongolia, China.

Diagnosis. On both fore- and hind wings, Rs_{1+2} shorter than Rs_{1a+1b}, Rs_{1+2} shorter than Rs_{3+4}, Rs and M forking at the same level and no spots or fasciae.

Description. Mainly based on Holotype, unless indicated as paratype. A well-preserved female adult fossil. Body 12 mm long. Forewing and hind wing overlapping almost entirely, but most of veins discernible. Thorax and abdomen preserved, but head poorly preserved. Legs poorly preserved, with only few fragments (Figs 1A, 2A, 2C–F).

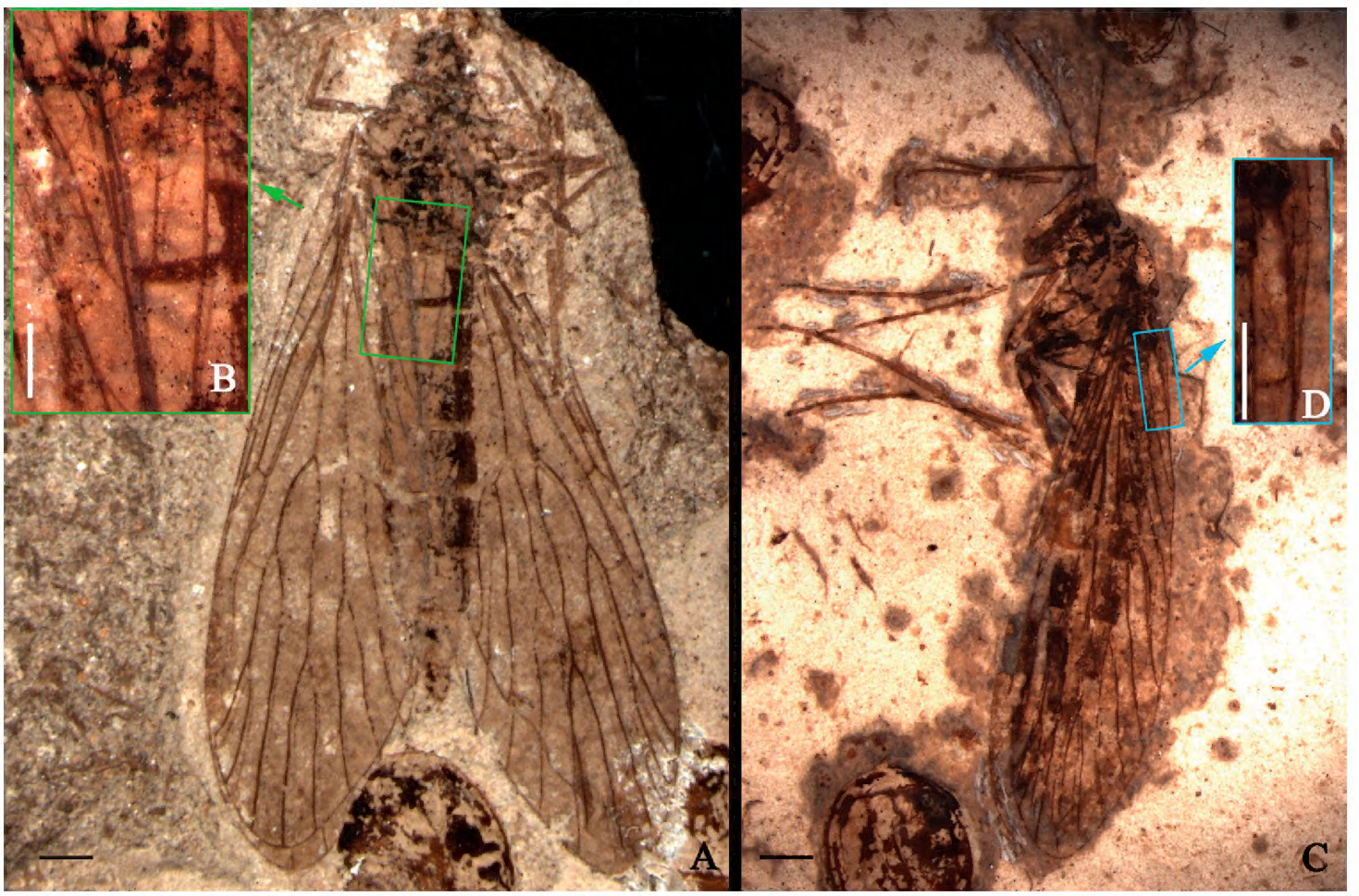

Figure 1. *Jurassipanorpa impunctata* gen. et sp. n., holotype, CNU-MEC-NN-2013006; paratype, CNU-MEC-NN-2013012 P/C. photos. **A** holotype **B** setae on forewings, under alcohol, outlined at rectangular frame in **A**; **C** paratype, under alcohol **D** setae on forewings, under alcohol, outlined at rectangular frame in **C**. Scale bars: 1 mm in **A**; 0.5 mm in **B, C**; 2 mm in **C**.

Head: Head capsule with downward extended mouthparts; compound eyes large and oval, three ocelli present (Figs 1A, 2A); Antennae filiform in paratype (Figs 1C, 2B).

Thorax: In dorsal view, 2.9 mm long, two setae on pronotum as preserved. Pronotum, mesonotum, metanotum clearly discernible. Meso- and metanotum about the same size; larger than pronotum.

Abdomen: In dorsal view, 9 mm long, tapering apically, with eleven visible segments; segments IX-XI more slender and shorter than segments II-VI. Cerci not preserved. Sterna visible in segments II-VI.

Legs: Densely covered with short setae, two long tibial spurs preserved in a mid leg, one tibial spur preserved in a fore leg and two hind legs in paratype (Figs 1C, 2B).

Wings: Venation similar to venation of *Panorpa.* Forewing (Figs 1A, 2A, B, C, D, F) 14 mm long with a maximal width of 4 mm, longer than the abdomen; Sc terminating at anterior margin near the middle of the wing; one distally located crossvein between Sc and R_1; R_1 long, branching and curving around pterostigma; one crossvein present between R_1 and Rs_1; Rs with five branches; Rs_1 forking into Rs_{1a} and Rs_{1b}; Rs_1 and Rs_{3+4} forking nearly at the same level; Rs_{1+2} forking proximad of Rs_{3+4} forking; one crossvein between Rs_{3+4} and M_{1+2}; Rs and M forking at the same level; M with four branches; M_{3+4} shorter than M_{1+2}; Cu_1 not fusing with M basally; one crossvein present between Cu_1 and Cu_2; 1A long, reaching posterior wing margin beyond the forking of Rs from

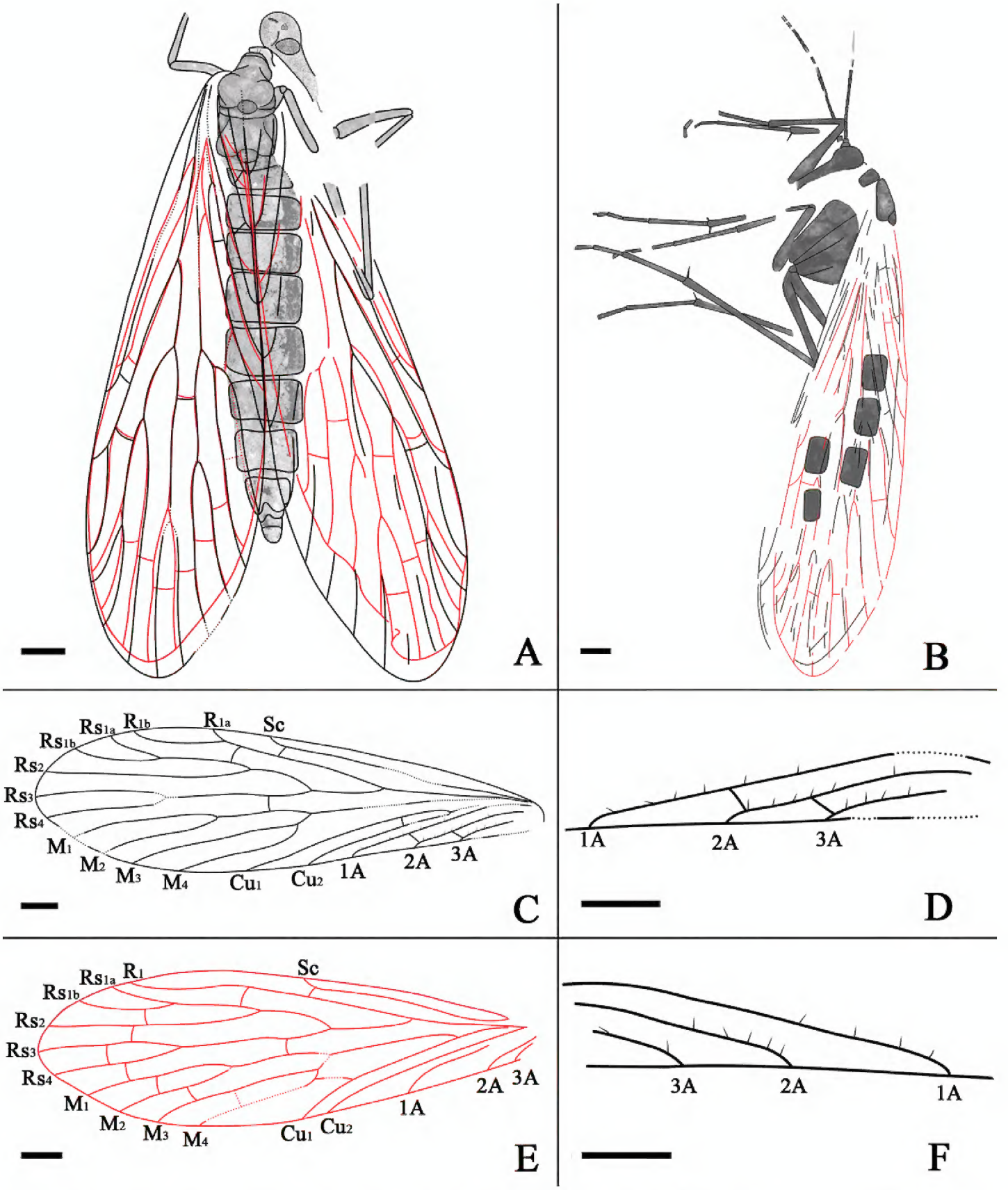

Figure 2. *Jurassipanorpa impunctata* gen. et sp. n. line drawings. **A** holotype **B** paratype **C** left forewing of the holotype **D** anal part of left forewing highlighting setae of the holotype **E** left hind wing of the holotype, crossvein between M_3 and M_4 is based on the right hind wing **F** right forewing highlighting setae of the holotype. Scale bars: 1 mm in **A**–**F**.

R_1; one crossvein between 1A and 2A; 2A and 3A long, one crossvein between 2A and 3A; long and robust setae ranging from 0.09 to 0.17 mm in length, present on veins 1A, 2A and 3A (Figs 1B, D, 2D, F). Hind wing (Figs 1A, 2A, E), 12.3 mm long with a maximal width of 3.9 mm, smaller than forewing distinctly, of similar shape and veins; Sc short, reaching anterior wing margin before one-half wing length; one crossvein

present between Sc and R_1; R_1 without forking; Rs with five branches; Rs and M forking at almost the same level; one crossvein present between R_1 and Rs_1; Rs_1 forking into Rs_{1a} and Rs_{1b}; one crossvein between Rs_{1b} and Rs_2; Rs_2 without forking; one crossvein between Rs_2 and Rs_3; Rs_{1+2} forking proximad of Rs_{3+4} forking; one crossvein between Rs_3 and Rs_4; M_{1+2} forking proximad of Rs_{3+4} forking; one crossvein between Rs_{3+4} and M_{1+2} and one crossvein between Rs_4 and M_1; M with four branches; one crossvein between M_1 and M_2; M_{3+4} shorter than M_{1+2}; one crossvein between M_2 and M_3 and between M_3 and M_4 respectively; Cu_1 coalesced with M basally; one crossvein between M_4 and Cu_1; no crossveins between anal veins.

Jurassipanorpa sticta Ding, Shih & Ren sp. n.

http://zoobank.org/73034C76-F459-48E5-A12C-EA1989478855

Figs 3, 4

Etymology. From the Greek *stiktos*, meaning spotted, referring to various spots and fasciae on wings.

Holotype. CNU-MEC-NN-2013007 P/C, part and counterpart, sex unknown, well- preserved fore- and hind wings, but abdomen indiscernible.

Paratype. CNU-MEC-NN-2013011, sex unknown, anal part of forewings well-persevered.

Locality and horizon. Jiulongshan Formation, late Middle Jurassic; Daohugou Village, Ningcheng County, Inner Mongolia, China.

Diagnosis. On both fore- and hind wings, Rs_{1+2} longer than Rs_{1a+1b} and Rs_{1+2} longer than Rs_{3+4}. Rs and M forking at the same level on forewing but Rs forking proximad of M forking on hind wing. All wings with scattered dark spots and fasciae.

Description. Mainly based on Holotype, unless indicated as paratype. A well-preserved adult fossil, sex unknown. Right forewing and hind wing nearly overlapping entirely, but most veins discernible, left forewing and right wings partially overlapping, left hind wing well preserved (Figs 3A, B, 4A).

Head: Head capsule with prolonged downward mouthparts as modern panorpids. Compound eyes large and oval; ocelli untraceable; antennae filiform, with 25 segments as preserved.

Thorax: poorly preserved (Figs 3A–C, 4A), only prothorax and part mesothorax recognizable. Few setae on tergum.

Legs: Densely covered with short setae; one mid leg not preserved; coxae and trochanters of all legs not preserved; femur and tibia long; two long tibial spurs present on a fore leg, one tibial spur present on a hind leg and one of them incomplete on a mid leg.

Abdomen: Indiscernible.

Wings: Forewing, 11 mm long with a maximum width of 3.9 mm, with scattered dark spots and fasciae (Figs 3A–C, 4A, C, E) with a different pattern from those of extant Panorpidae. Sc long, reaching anterior wing margin beyond one-half of wing length; one crossvein between Sc and R_1 located nearly of mid-length of Sc; R_1 long

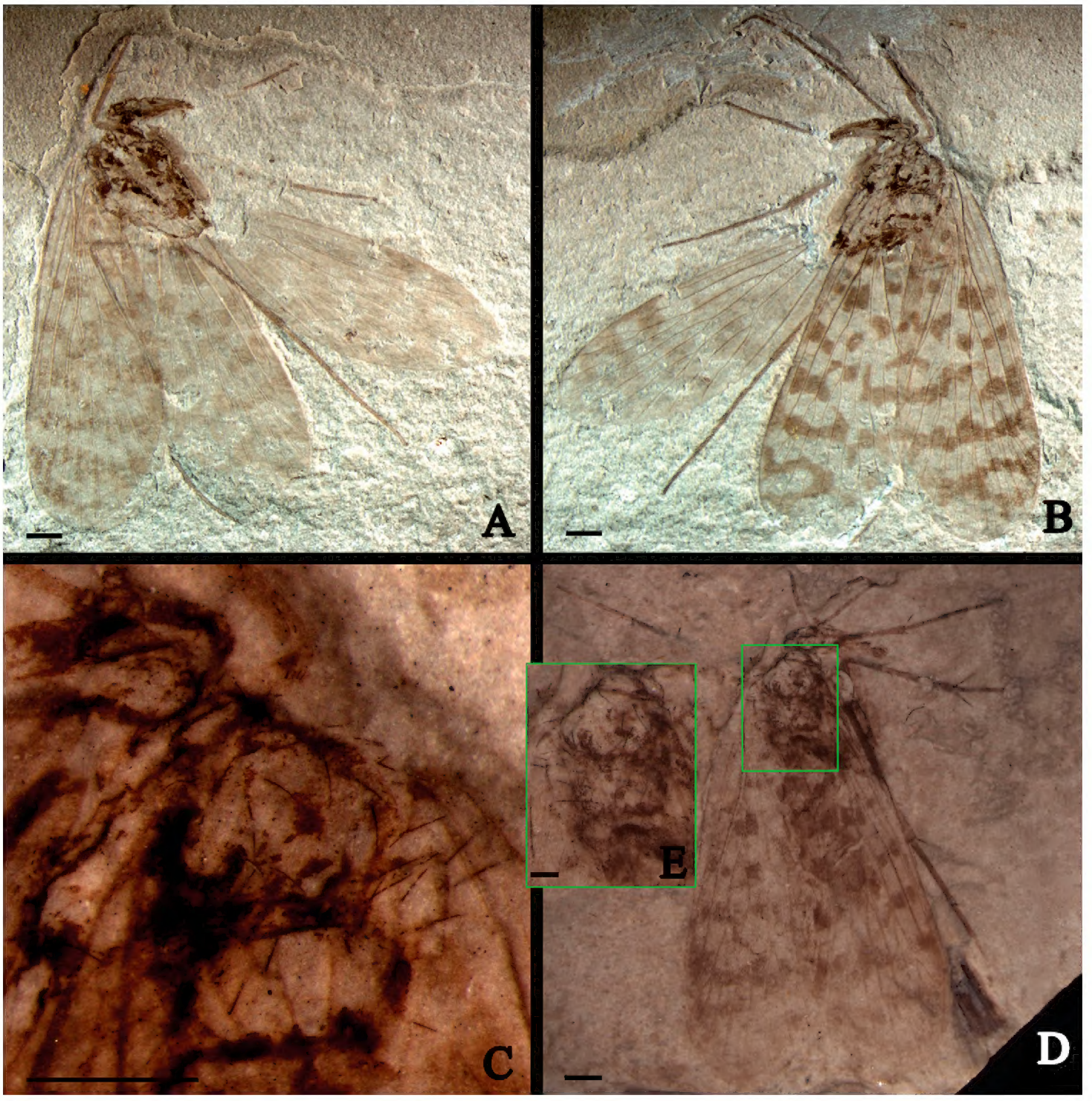

Figure 3. *Jurassipanorpa sticta* sp. n., holotype, CNU-MEC-NN-2013007 P/C; paratype, CNU-MEC-NN-2013011. photos. **A** part of the holotype **B** counterpart of the holotype **C** anal part of forewings of the holotype, under alcohol **D** paratype, under alcohol **E** setae on forewings, under alcohol, outlined at rectangular frame in D. Scale bars: 1 mm in A–D, 0.5 mm in **E**.

with two branches; one crossvein between R_1 and Rs_1; Rs with five branches, originating from R_1 nearly basal 1/3 of forewing length; Rs_1 forking into Rs_{1a} and Rs_{1b}; one crossvein between Rs_{1b} and Rs_2; two crossveins between Rs_2 and Rs_3; Rs_{1+2} forking distad to Rs_{3+4} forking; one crossvein between Rs_3 and Rs_4; Rs and M forking at almost the same level; one crossvein between Rs_4 and M_1; M with four branches; one crossvein between M_1 and M_2; M_{3+4} shorter than M_{1+2}; one crossvein between M_2 and M_3; Cu_1 not fusing with M basally, but joining M_4 by a oblique crossvein; Cu_1 fusing with Cu_2 basally and one crossvein between Cu_1 and Cu_2; 1A long, reaching posterior wing margin distad to the origination of Rs from R_1; 2A and 3A short; long and robust

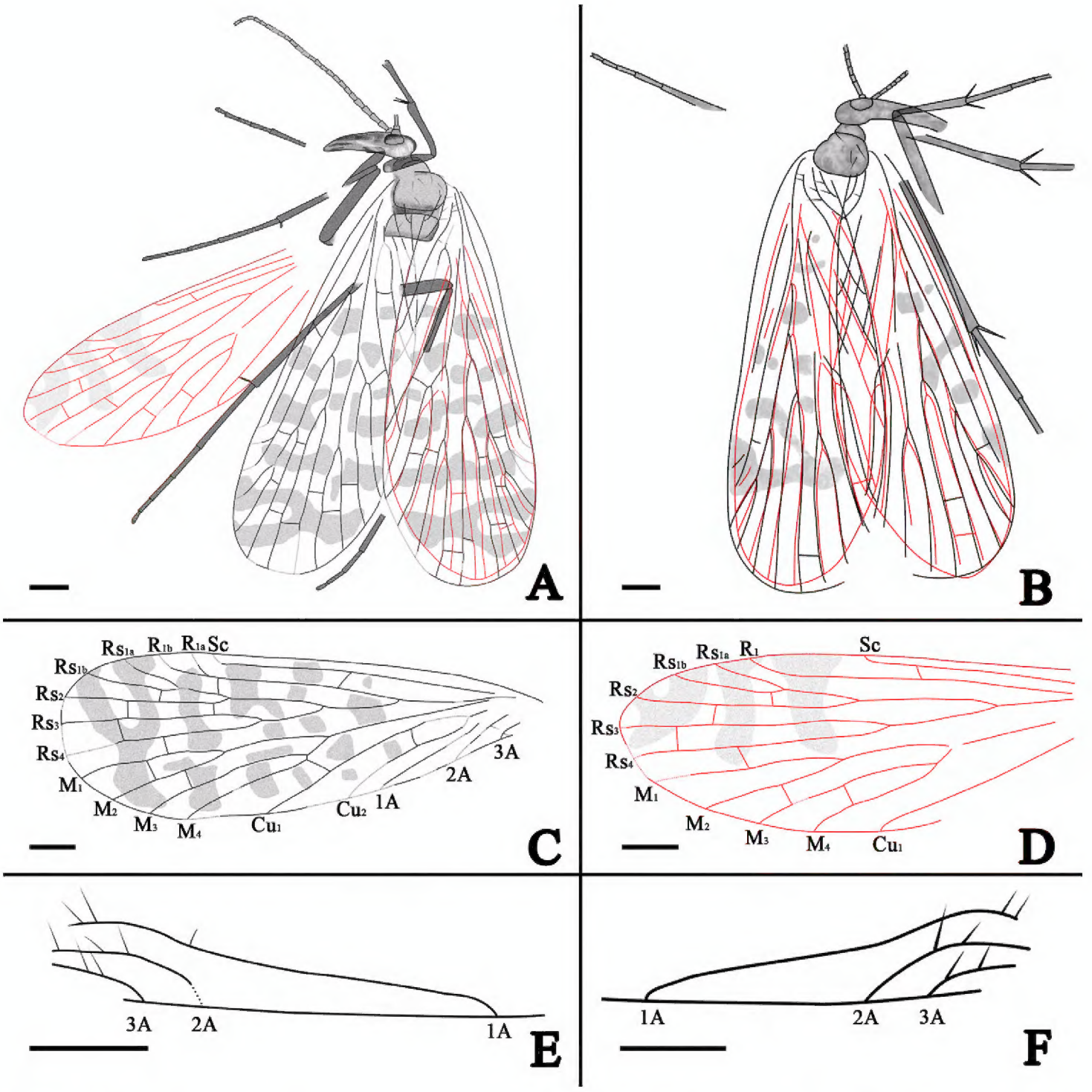

Figure 4. *Jurassipanorpa sticta* sp. n. line drawings. **A** holotype **B** paratype **C** left forewing of the holotype **D** left hind wing of the holotype **E** anal part of right forewing highlighting setae of the holotype **F** left forewing highlighting setae of the paratype. Scale bars: 1 mm in **A–F**.

setae ranging from 0.15 to 0.38 mm in length, present on veins 1A, 2A and 3A of holotype and paratype (Fig. 4E, F). Left hind wing extended, right hind wing covered by the right forewing, incomplete; hind wing 9 mm long with a maximal width of 3.2 mm, smaller than forewing distinctly, of similar shape and veins (Figs 3A, B, 4A, D); but fasciae much reduced. Sc short, reaching anterior wing margin beyond one-half of wing length; one crossvein between Sc and R_1; R_1 long without forking; Rs with five branches; Rs_1 forking into Rs_{1a} and Rs_{1b}; one crossvein between Rs_{1b} and Rs_2; Rs_1 shorter than Rs_{1+2}; one crossvein between Rs_2 and Rs_3; Rs_{1+2} forking distad to Rs_{3+4} forking; one crossvein between Rs_3 and Rs_4; M furcating distad to the Rs forking; one crossvein between Rs_4 and M_1; M with four branches; one crossvein between M_2 and

M_3; M_{3+4} shorter than M_{1+2}; one crossvein between M_3 and M_4; Cu_1 coalesced with M basally; no crossveins present between M and Cu_1; anal veins not discernible on hind wing due to poor preservation.

Comparison. *J. sticta* sp. n. is differentiated from *J. impunctata* gen. et sp. n. by the following characters: (1) *J. sticta* with various spots and fasciae (vs. *J. impunctata* without spots and fasciae); (2) Rs_{1+2} longer than Rs_{1a+1b} (vs. Rs_{1+2} shorter than Rs_{1a+1b}); (3) Rs_{1+2} longer than Rs_{3+4} (vs. Rs_{1+2} shorter than Rs_{3+4}) (4) Rs and M forking at the same level on forewing, but Rs furcating proximad of M forking on hind wing (vs. Rs and M forking at the same level on both fore- and hind wing).

Discussion

In the vast insect fossil collection at the Capital Normal University (> 250,000 fossil insect specimens), we have collected only four panorpid fossils so far from the Daohugou locality. Informal survey of the Mecoptera collection indicates that specimens of Nannochoristidae are abundant, followed by many specimens of Orthophlebiidae, Bittacidae, and Cimbrophlebiidae, then, low numbers of Choristopsychidae, Mesopsychidae, Aneuretopsychidae, Pseudopolycentropodidae, and Eomeropidae, while very rare for Panorpidae. It is interesting to note that the rarity of Panorpidae during the Middle Jurassic of northeastern China is in contrast to their dominance in the Recent world fauna of Mecoptera (about 66% of all extant species).

Described fossil records of the Panorpidae in Mesozoic are extremely rare. Up to now, only one species, *Solusipanorpa gibbidorsa* Lin, 1980, has been described. However, we consider the holotype of *S. gibbidorsa* as not sufficiently preserved to be attributed to Panorpidae nor to any other family, and regard *S. gibbidorsa* as Mecoptera incertae sedis. Eight species in two genera: *Panorpa* Linnaeus, 1758, and *Baltipanorpa* Krzemiński, 2012, have been reported from the Eocene and Oligocene, however Carpenter stated that "*Panorpa rigida* Scudder, from the Florissant shales, is too incompletely preserved to permit even family classification." and "*Panorpa arctiiformis* Cockerell, also from the Florissant shales, is undoubtedly a member of the family Panorpidae, but I have not seen the type specimen and there is nothing in the description to indicate its affinities." (Carpenter 1931, Carpenter 1954, Willmann 1989, Krzemiński and Soszyńska-Maj 2012, Archibald et al. 2013). *Jurassipanorpa impunctata* gen. et sp. n. and *J. sticta* sp. n. described in this study are the earliest fossil panorpids in the world hitherto. The holotypes of these two new species of *Jurassipanorpa* gen. n. are well-preserved, including both wings and most of the body. New information from these two new species enhances our understanding of the morphological characters of Panorpidae and diversity of Mecoptera during the late Middle Jurassic.

Based on studies of these two new species and documented species of other representative panorpids, we compare and summarize six key forewing characters in Table 1. A combination of the following characters enables us to distinguish the new genus from all other described genera of Panorpidae: (1) R_1 with two branches in

Table 1. Comparison of fossil and extant genera of Panorpidae with six key forewing characters.

	Genus	Species	Position of Sc reaching anterior margin	Branches of R_1	Branches of Rs_1	position of 1A reaching the posterior margin	number of crossveins between 1A and 2A	number of crossveins on forewing	Comments
extant genera	*Panorpa* Linnaeus, 1758	*P. communis* L. 1758	beyond the middle of wing	1 (2 only in rare cases)	2–3	far beyond the forking of Rs from R_1	2	about 22	
	*Neopanorp*a Weele, 1909	*N. appendiculata* (Westwood, 1846)	beyond the middle of wing	1	2	not beyond the forking of Rs from R_1	1	about 23	
	Leptopanorpa MacLachlan, 1875	*L. ritsemae* MacLachlan, 1875	beyond the middle of wing	1	2	at same level as the forking of Rs from R_1	1	about 27	wings are slender and much narrower basally
	*Sinopanorp*a Cai and Hua, 2008	*S. tincta* (Navas, 1931)	beyond the middle of wing	1	3	far beyond the forking of Rs from R_1	2	about 22	
	Furcatopanorpa Ma & Hua, 2011	*F. longihypovalva* (Hua & Cai, 2009)	near the middle of wing	2 (fore- and hind wings)	2	far beyond the forking of Rs from R_1	3	about 26	wings held roof-like over the abdomen at rest.
	Dicerapanorpa Zhong & Hua, 2013	*D. magna* (Chou, 1981)	beyond the middle of wing	1 (but 2 in hind wings of some cases)	2	far beyond the forking of Rs from R_1	2	about 26	
fossil genera	*Baltipanorpa* Krzemiński, 2012, Eocene	*B. damzeni* Krzemiński, 2012	before the middle of wing	2	2	at same level as the forking of Rs from R_1	3	about 26	
	Jurassipanorpa gen. n., Middle Jurassic	*J. impunctata* gen. et sp. n.	at the middle of wing	2	2	far beyond the forking of Rs from R_1	1	6	no spots and fasciae
		J. sticta sp. n.	beyond the middle of wing	2	2	far beyond the forking of Rs from R_1	0	11	spots and fasciae much different from extant Panorpidae

forewing – same as *Baltipanorpa*, *Furcatopanorpa* and a rare few species of *Panorpa*, but different from all other genera with only one branch; (2) Rs_1 with two branches of Rs_{1a} and Rs_{1b} – different from *Sinopanorpa* with 3 branches; (3) 1A reaching posterior margin distad of the forking of Rs from R_1 in forewing – same as *Panorpa*, *Sinopanorpa*, *Furcatopanorpa*, *Dicerapanorpa*, and *Baltipanorpa*, in contrast to significantly shortened 1A in *Neopanorpa* and *Leptopanorpa*; (4) no crossveins or only one crossvein between 1A and 2A on forewing – different from almost all other genera of Panorpidae, *Neopanorpa* and *Leptopanorpa* (one crossvein), *Panorpa* (one or two crossveins), *Sinopanorpa,* and *Dicerapanorpa* (two crossveins), *Baltipanorpa* and *Furcatopanorpa* (three crossveins); (Byers 1967, Cai et al. 2008, Ma and Hua 2011, Krzemiński and Soszyńska-Maj 2012, Zhong and Hua 2013).

We found that the wing venation of this family is comparatively stable, that is, Sc not forking, Rs_2, Rs_3, Rs_4 without forking, and M with 4 branches. However, Rs_1 is rather variable, typically, Rs_1 has two branches, but, some with three branches such as *Sinopanorpa,* while three Mexican extant species *Panorpa dividilacinia, P. mixteca, P. umbricola* have only a single Rs_1 (Carpenter 1992, Bicha 2006, Cai et al. 2008).

Most panorpids have M_4 bending basally in forewings, that is, M_3 is a straight branch while M_4 is derived from M_3 with a basal bending. However, this character is not obvious for some extant panorpids, such as *Panorpa wangwushana* Huang, Hua and Shen, 2004 (Huang et al. 2004). On the other hand, most panorpodids have M_3 bending basally in forewings, that is, M_4 is a straight branch while M_3 is derived from M_4 with a basal bending. However, *Panorpodes colei* Byers, 2005 is an exception to this typical panorpodid character (Byers 2005). *J. impunctata* gen. et sp. n. has M_4 bending basally in forewing (Figs 2A, C), but *J. sticta* sp. n. does not have obvious M_4 bending basally, nor M_3 bending basally (Figs 4A, C). Hence, we propose that M_4 or M_3 basal bending is variable in both Panorpidae and Panorpodidae.

All four specimens of *J. impunctata* gen. et sp. n. (Figs 1B, D, 2D, F) and *J. sticta* sp. n. (Figs 3C, E, 4E, F) have remarkable long and robust setae on anal veins of the forewings that are not known for any other described fossil or extant panorpid species. Unlike these of *Jurassipanorpa* gen. n., setae on veins of extant species of Panorpidae as well as of Mesozoic Orthophlebiidae are usually more dense, shorter and decumbent unidirectionally and look similar to microtrichia on the wing membrane (Tillyard 1933, Webb and Penny 1979, Whalley 1985, Whalley 1986). These setae of the new genus, with lengths ranging from 0.09 to 0.38 mm, are similar in appearance to the piliform scales, ranging from 0.12 to 0.21 mm in lengths, present on the hind wing veins of *Akainalepidopteron elachipteron* Zhang, Shih, Labandeira & Ren, 2013 of Lepidoptera (Zhang et al. 2013), or to robust bristles ("dinotrichia") on the basal anterior margin of forewings on the Recent *Notiothauma reedi* and fossil *Tsuchingothauma shihi* and *Jurathauma simplex* (Eomeropidae) (Crampton 1930, Ren and Shih 2005, Zhang et al. 2011). The wing scales have been used as a diagnostic character for Lepidoptera, while also found in some forewings of Trichoptera (Kristensen 1984, Grimaldi 1999, Zhang et al. 2013). However, it is unlikely that these setae are homologous to piliform scales because scales have not been reported for Panorpidae. Since these setae are lo-

cated only on anal veins of the forewings while all pointing anteriorly, we hypothesized that they might have been used for wing coupling. But, we could not find any associated structures preserved on the anterior part of the hind wings on these specimens. Hence, the function of these setae remains enigmatic.

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